TIME BUDGETS AND THE ADAPTIVENESS OF POLYANDRY IN NORTHERN JACANAS

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ABSTRACT.—Time budgets of polyandrous Northern Jacanas (*Jacana spinosa*) were studied at a 2.8-ha pond in Costa Rica from Jan.–Dec. 1974. Time budgets differed significantly depending on reproductive condition, sex, location, and time of day. Although similar prior to egg laying, male and female time budgets diverged greatly when eggs or chicks were present. At that time, males reduced foraging, other somatic behaviors, and time spent off-the-pond as they assumed major responsibility for parental care, which consumed much of the early morning and late afternoon. Females, which were never seen incubating and were rarely seen brooding, maintained a high proportion of time spent foraging throughout the day and year. Females spent more time in territories where chicks were present, resulting in increased interspecific aggression, resting, and walking as they provided direct and potential predator protection. After egg laying, females reduced time spent foraging and increased time spent resting. Females helped males by brooding and accompanying chicks at times when food availability was apparently low. Females did not reduce their total foraging time in territories containing chicks. These data best support the replacement clutch hypothesis and support neither the female energetic stress nor the uniparental care hypotheses for the adaptiveness of classical polyandry in the Northern Jacana. Insufficient data exist to conclude whether a single explanation for the evolution of classical polyandry is possible for all species exhibiting some form of this mating system. *Received 4 Feb. 1991, accepted 10 April 1991.*

Avian polyandry takes two basic forms (Oring 1986). In classical polyandry, females engage in separate reproductive efforts with each of several males. In cooperative polyandry, several males share in a single reproductive effort by a female. Although cooperative polyandry is an important form of this mating system, only classical polyandry is considered in the present paper, and all further references to polyandry should be regarded as referring only to classical polyandry.

Classical polyandry is known to be the predominant mating system in only two avian species: the Spotted Sandpiper (*Actitis macularia*) (Hays 1972, Oring and Knudson 1972) and the Northern Jacana (*Jacana spinosa*) (Jenni and Collier 1972). Polyandrous mating relationships also occur infrequently in several other shorebirds that are basically monogamous (for reviews see Jenni 1974, Emlen and Oring 1977, Erckmann 1983, Lenington 1984, Oring 1986, Colwell and Oring 1988).

Hypotheses for the adaptiveness of classical polyandry can be grouped into three ecological arguments. Female energetic stress hypotheses sug-

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gest that limited food and laying-induced energy depletion of females interact to favor paternal care of the young. Food scarcity might preclude any sharing of incubation by the female (Graul et al. 1977, Lenington 1980, 1984), or it might only make it less possible for the female than for the male to do all parental care (Maynard Smith 1977, Ashkenazie and Safriel 1979, Erckmann 1981). If food supplies fluctuate, periods of scarcity would favor desertion by the female, and temporary, infrequent periods of superabundance would allow multiple clutching by the female for the same or a different male (Graul 1973, 1976; Lenington 1984).

Uniparental care hypotheses assert only that sometimes uniparental care can be more successful than biparental care but do not argue for one type of polygamy over another (Pitelka et al. 1974). Uniparental care might be more successful if frequent trade-offs at the nest increased nest predation or if there were significant competition for food between parents or between parents and offspring. The increase in reproductive fitness realized through the anti-predator or feeding benefits gained by desertion of one parent would have to be greater than any decrease in fitness resulting from uniparental care.

The replacement clutch hypothesis argues that excessive clutch loss makes polyandry adaptive for both sexes if the female, freed from parental duties, can forage more and rapidly provide replacement clutches (Jenni 1974, Emlen and Oring 1977). The male and the female would both benefit by another chance at reproduction, and in addition, the female could produce clutches for additional males.

A major problem associated with testing these hypotheses is the difficulty in measuring parental investment, particularly in terms of the cost to the parent's ability to invest in other offspring (Trivers 1972). Although relative energetic investments in the gametes can be compared, the amount of time and energy invested in all aspects of reproduction need to be analyzed (Brunton 1988). However, only a few such studies have been done on shorebirds. Time and/or energy budget data for breeding individuals of non-polyandrous species are reported by Gibson (1971, 1978), Ashkenazie and Safriel (1979), Lenington (1980), Burger (1981), Brunton (1988), and Purdy and Miller (1988). Similar studies of polyandrous species include only those by Maxson and Oring (1980) on a population of Spotted Sandpipers and Osbourne and Bourne (1977) on one pair of Wattled Jacanas (*Jacana jacana*).

Of the polyandrous shorebirds, only the tropical jacanas typically exhibit simultaneous polyandry. Female Spotted Sandpipers occasionally pair with more than one male simultaneously (Oring and Maxson 1978), but sequential pairing is much more common (Hays 1972, Oring and Knudson 1972). The best known jacana is the Northern Jacana; a detailed

description of polyandry in this species is given by Jenni and Collier (1972) and Jenni and Betts (1978). Males maintain individual territories. Breeding females are 75% larger than males and defend territories encompassing those of 1–4 males. Sex role reversal is nearly complete, with males assuming most of the nest building and parental care. Females maintain pair bonds with each male, copulating frequently with each, laying eggs for some, helping defend male territories, and providing predator protection for eggs and chicks.

In this paper we describe time budgets of a polyandrous population of Northern Jacanas. The paternal care system causes gross differences in the reproductive time budgets of the two sexes, parts of which we have reported previously (Jenni and Betts 1978). Here, we are also interested in adjustments of time allocation related to differences in location and time of day. We show how these time budgets relate to a polyandrous system and we use the time budget data to help evaluate how hypotheses of the adaptiveness of polyandry apply to this species.

METHODS

The study area, described in detail by Jenni and Collier (1972), was a shallow 2.8-ha pond at 600 m elevation near Turrialba, Costa Rica. The pond was bordered by lawn and patches of trees. Parts of the edge were overgrown by heavy stands of papyrus (*Cyperus papyrus*), but the majority of the pond was covered by water lilies (*Nymphaea ampla*) and other low vegetation which allowed observation of the birds.

Time budget data were gathered Jan.–Dec. 1974. Boundaries of the six male territories remained stable throughout this period even though one male was replaced. Early in the year two boundary changes occurred among the females as territory ownership shifted from one monandrous, one biandrous, and one triandrous female to two triandrous females. In the remaining nine months, one of these triandrous females was replaced once, but the territory boundaries remained stable. Although this population was small, we believe its social system is typical for Northern Jacanas at other permanent ponds or lakes. This population was studied from 1963 to 1976, and considerable turnover in individual birds occurred with no change in the general social structure. Also, both of us observed other, larger populations where we noticed no major differences in behavior.

We made observations through binoculars and spotting scopes from various locations around the pond. The birds were habituated to observers which made blinds unnecessary. All individuals were marked with colored leg bands. Sex was determined from size (Jenni 1974) and observations of copulation and egg laying.

We gathered instantaneous time budget data (Altmann 1974) on territory holders during all phases of their reproductive cycle. Birds were chosen for observation on the basis of reproductive condition in order to maximize sample size. Individuals in reproductive conditions under-represented in the data were chosen preferentially over others. Two to three birds could be observed at once. Data were collected at two-min intervals in two-h time blocks. An individual "data-day" consisted of observations made on one–three consecutive calendar days. When observations extended more than one day, the two-h time blocks were distributed such that all daylight hours were sampled. Day length varied from about 11.5

to 12.5 h. Observations were spread evenly throughout the year. We accumulated 86 data-days (31,428 observations) on the seven males and 42 data-days (15,633 observations) on the five females that held territories at some time during 1974. Proportions of instantaneous observations are estimates of the percentage of daylight hours spent in particular behavioral categories and are reported here as percentages of observation time.

For each instantaneous sampling point we recorded the location and behavior of the bird, or if it was out of sight, a subjective analysis of weather conditions and any other observations worth noting. For analysis, behaviors were combined into the following 12 categories which are comparable with those used by Maxson and Oring (1980) for the Spotted Sandpiper and by Brunton (1988) for the Killdeer (*Charadrius vociferus*). For some analyses, categories were further grouped as somatic, mating, and parental behaviors, following Brunton (1988).

Somatic behaviors include: (1) foraging—walking or standing with bill lowered and frequently pecking at food or poking or peering at vegetation; (2) preening—grooming feathers, bathing, scratching, or stretching; (3) resting—sitting or standing; (4) flying—normal horizontal flight; and (5) walking—walking with bill horizontal, without pecking at food or peering at vegetation and not in company of chicks.

Mating behaviors include: (1) nest building—pulling at vegetation, picking up and throwing rearward bits of vegetation, push-stepping on the nest platform, or poking bill into nest site; (2) presenting-mounting—precopulatory displaying by either sex and unsuccessful mountings; (3) copulating—mountings in which successful cloacal contact is apparently established; and (4) intraspecific aggression—aggressive and appeasement interactions involving other jacanas, most often associated with territorial defense.

Parental behaviors include: (1) incubating—sitting on the nest when eggs are present, (2) walking-with-chicks—accompanying the chicks as the latter feed, (3) brooding—sheltering one or more chicks with the body or wings, and (4) interspecific aggression—aggressive interactions involving potential predators.

Data for males were grouped into four reproductive conditions: (1) precopulation (16 days, 5726 observations)—male had neither eggs nor chicks less than 10 weeks old and was not copulating with his mate; (2) copulation (29 days, 10,686 observations)—male had neither eggs nor chicks less than 10 weeks old and was copulating with his mate; (3) incubation (16 days, 5911 observations)—male had eggs; and (4) brooding (25 days, 9105 observations)—male had chicks less than 10 weeks old. Data for females were grouped into five categories: (1) precopulation (4 days, 1431 observations)—female was not copulating with any of her males and had no mates with eggs or chicks; (2) copulation (19 days, 7087 observations)—female was copulating with one or more males and had no mates with eggs or chicks; (3) with-eggs-only (seven days, 2568 observations)—female had at least one incubating mate and may or may not have been copulating with her other males; (4) with-chicks-only (7 days, 2507 observations)—female had at least one brooding mate and may or may not have been copulating with her other males; and (5) with-eggs-and-chicks (five days, 1822 observations)—female had at least one incubating and one brooding mate and may or may not have been copulating with her third male.

Data were grouped into six time periods: dawn–08:00, 08:00–10:00, 10:00–12:00, 12:00–14:00, 14:00–16:00, and 16:00–dusk, CST. The length of the first and last periods varied due to seasonal changes in dawn and dusk times, but averaged about two hours each. Because data are reported as percentages of observation time, this variation is probably unimportant.

Time budget data were analyzed for variation related to reproductive condition, sex, location, and time of day. Nonparametric statistics were used to test for significance to avoid assuming that data were normally distributed with equal variances. Except where noted, either the Kruskal-Wallis one-way ANOVA or the Mann-Whitney *U*-test were used (Siegel 1956). Sample size is the number of data-days analyzed.
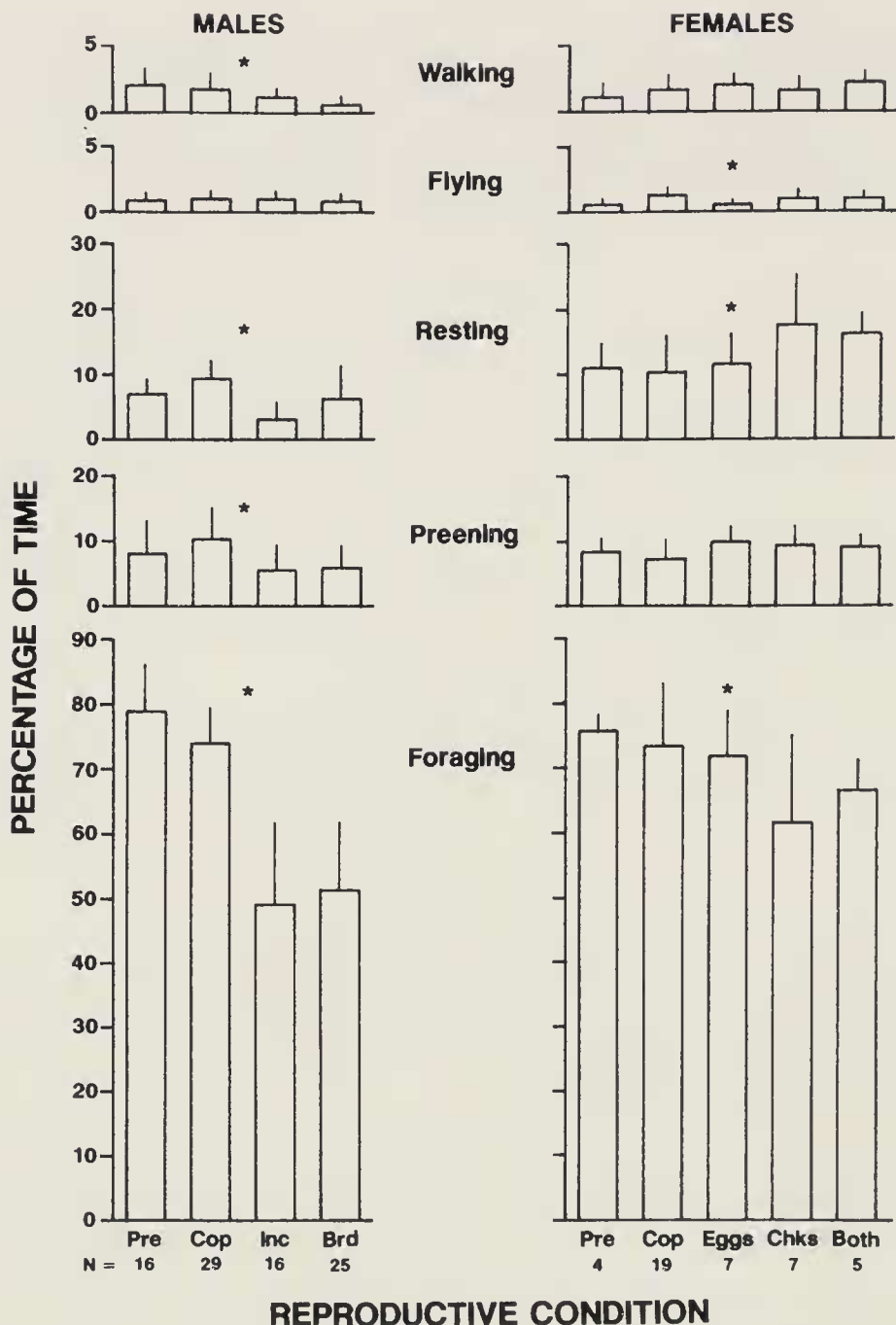
FIG. 1. Percentage of time males and females spent performing somatic behaviors as a function of reproductive condition. Pre = precopulation period, Cop = copulation period, Inc = incubation period, Brd = brooding period, Eggs = with-eggs-only period, Chks = with-chicks-only period, Both = with-eggs-and-chicks period. Statistical significance: * = $P \leq 0.05$ that there was no difference between reproductive conditions in the percentage of time spent in that behavioral category.

RESULTS

The polyandrous relationships of females and the monogynous relationships of males resulted in different reproductive cycles for the two sexes. The situation was especially complex for females whose mates could all be in different reproductive conditions. The pervasive differences between the sexes make it necessary to discuss male and female time budgets separately.

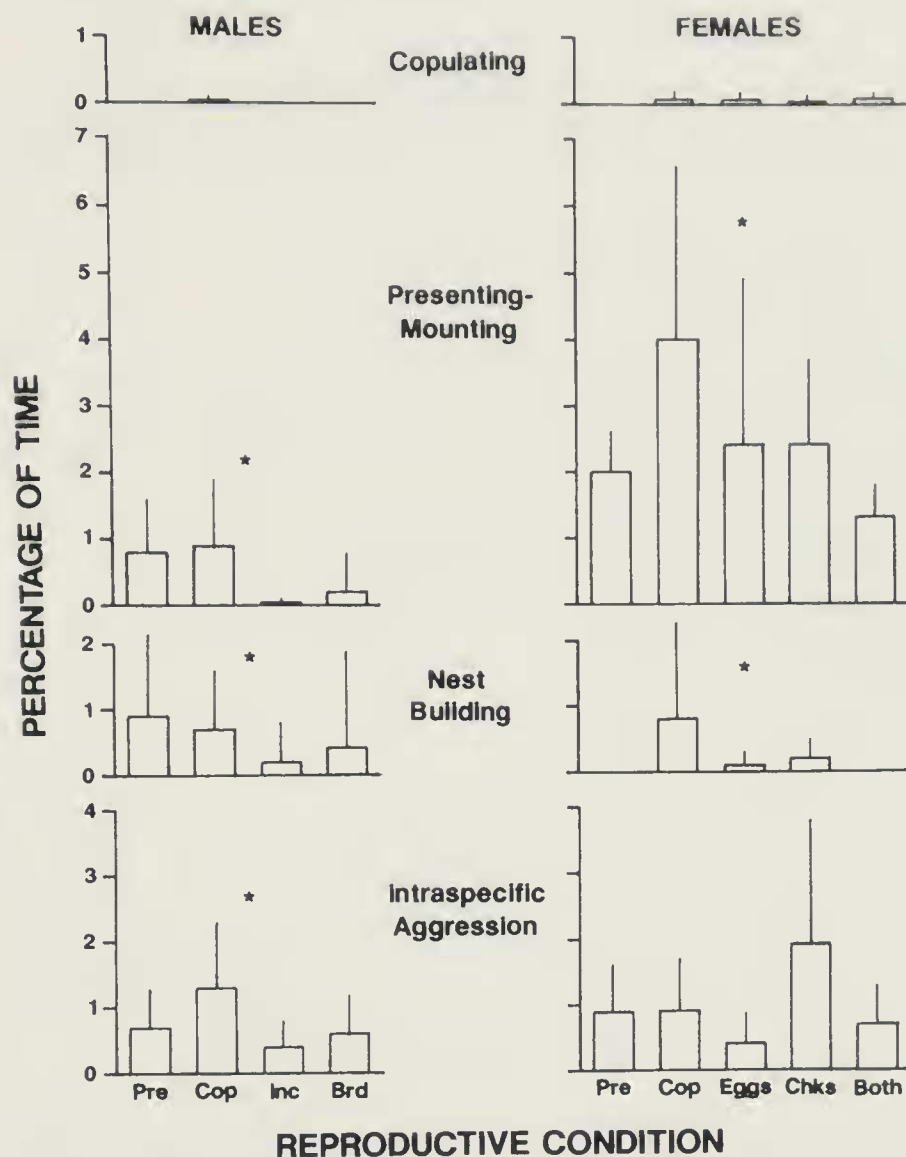*Reproductive condition differences.*—The amount of time spent in most

FIG. 2. Percentage of time males and females spent performing mating behaviors as a function of reproductive condition. Abbreviations, statistical significance, and sample sizes as in Fig. 1.

behavioral categories varied significantly with reproductive condition for both sexes (Figs. 1–3). Somatic behaviors consumed nearly 97% of the males' time prior to receiving a clutch (Fig. 1). Although never exceeding 3% of the males' time, mating behaviors occurred significantly more often prior to receiving a clutch, as would be expected (Fig. 2). Intraspecific aggression, highest in males during the copulation period, was primarily in defense of territory (Fig. 2).

Time budgets of males changed most drastically once eggs or chicks were present (Figs. 1–3). Males performed all observed incubation and most brooding, which occupied 39% and 26% of their time during the respective periods (Fig. 3). Males also did most of the walking-with-chicks (Fig. 3). Interspecific aggression, mostly directed at potential predators, was highest for brooding males (Fig. 3).

The increased time devoted to parental activities by males resulted in reduced time spent in most somatic activities (Fig. 1). Foraging time, in
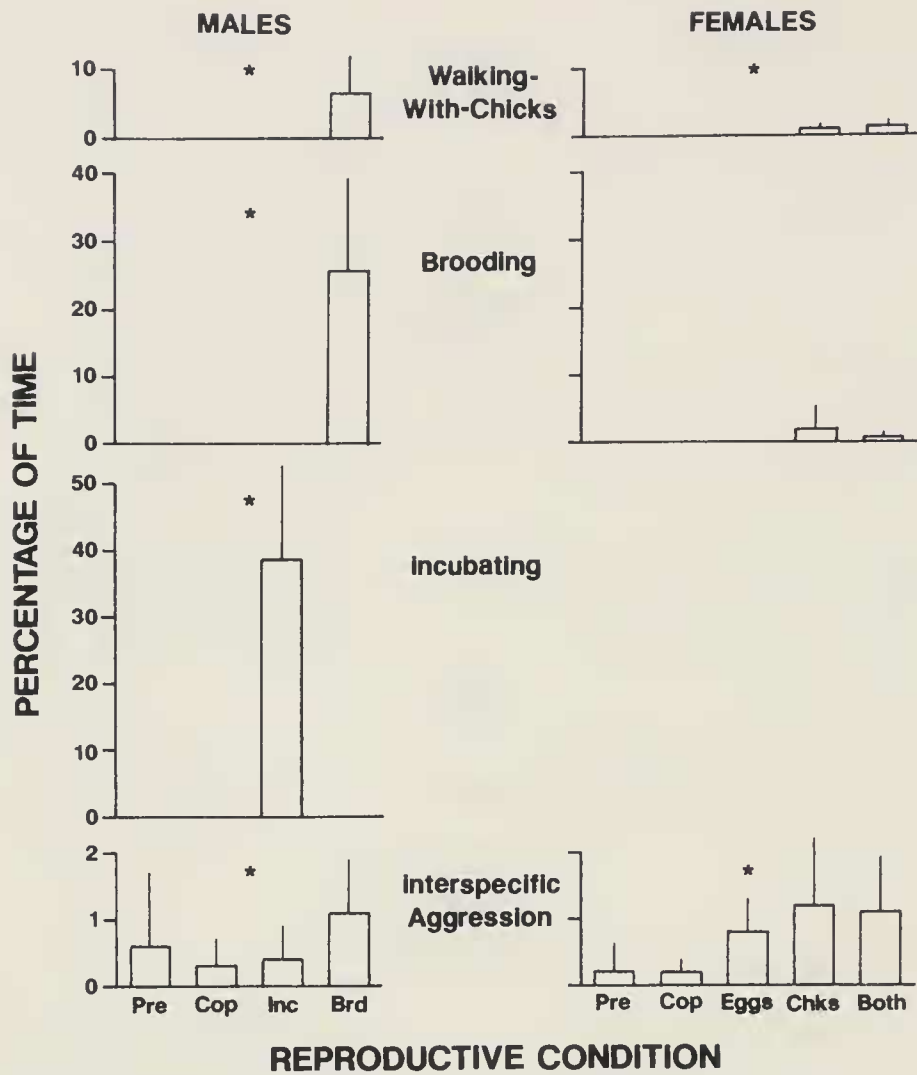
FIG. 3.   Percentage of time males and females spent performing parental behaviors as a function of reproductive condition. Abbreviations, statistical significance, and sample sizes as in Fig. 1.

particular, decreased by about one-third during the incubation and brooding periods. Preening, resting, and walking also were less frequent (Fig. 1). Males sometimes foraged, preened, and rested in the vicinity of chicks, providing non-overt predator protection for the chicks as well as fulfilling somatic functions for the males.

The effects of change in reproductive condition on the time budgets of females were less obvious than for males. Mating behaviors were most frequent before males received clutches but continued between females and those mates not yet having eggs or chicks (Fig. 2). Female parental behavior was largely anti-predator in nature, although females occasionally brooded and walked-with-chicks (Fig. 3). Interspecific aggression by females was highest when at least one of their mates had eggs or chicks (Fig. 3). Foraging by females was high regardless of reproductive condition but decreased once chicks were present when resting and walking increased (Fig. 1). Like males, females also performed some of their somatic behaviors close enough to the chicks to help provide predator protection.

Sex differences.—The data in Figs. 1–3 were examined for differences between the sexes (Table 1); we judged the with-eggs-only and with-chicks-

TABLE 1

STATISTICAL SIGNIFICANCE OF SEX DIFFERENCES IN TIME BUDGETS DURING DIFFERENT REPRODUCTIVE CONDITIONS. VALUES ARE PROBABILITIES; NS = $P > 0.05$

Behavioral category	Reproductive condition			
	Pre-copulation	Copulation	Incubation/with eggs only	Brooding/with chicks only
N (male, female) =	16, 4	29, 19	16, 7	25, 7
Somatic behaviors				
Foraging	NS	NS	≤0.001	≤0.05
Preening	NS	≤0.05	≤0.01	≤0.05
Resting	≤0.05	NS	≤0.001	≤0.001
Flying	NS	<0.05	≤0.05	·NS
Walking	NS	NS	≤0.05	≤0.01
Mating behaviors				
Intraspecific aggression	NS	NS	NS	NS
Nest building	≤0.05	NS	NS	NS
Presenting-mounting	≤0.01	≤0.001	≤0.01	≤0.001
Copulating	—	NS	≤0.01	NS
Parental behaviors				
Incubating	—	—	≤0.001	—
Walking with chicks	—	—	—	≤0.001
Brooding	—	—	—	≤0.001
Interspecific aggression	NS	NS	NS	NS
No. of categories with significant differences	3/9	3/10	8/11	7/12

only periods of the females as most appropriate for comparison with the incubating and brooding periods, respectively, of the males. Prior to egg-laying the time budgets of both sexes were similar, differing only in low-frequency behaviors (flying, nest building, and presenting-mounting) or in low-energy-demanding behaviors (preening and resting).

However, once eggs or chicks were present the time budgets of males and females diverged greatly (Table 1). Males spent 39% of their time incubating while females were never observed incubating, and males brooded and walked-with-chicks 26% and 7% of the time, respectively, compared to only 2% and 1% for females with-chicks-only (Fig. 3). Conversely, incubating and brooding males spent significantly less time than females in most somatic behaviors (Table 1). Time spent in mating behaviors remained infrequent once eggs or chicks were present and did not differ significantly between the sexes, except that females continued copulating and presenting-mounting with their other mates (Fig. 3).
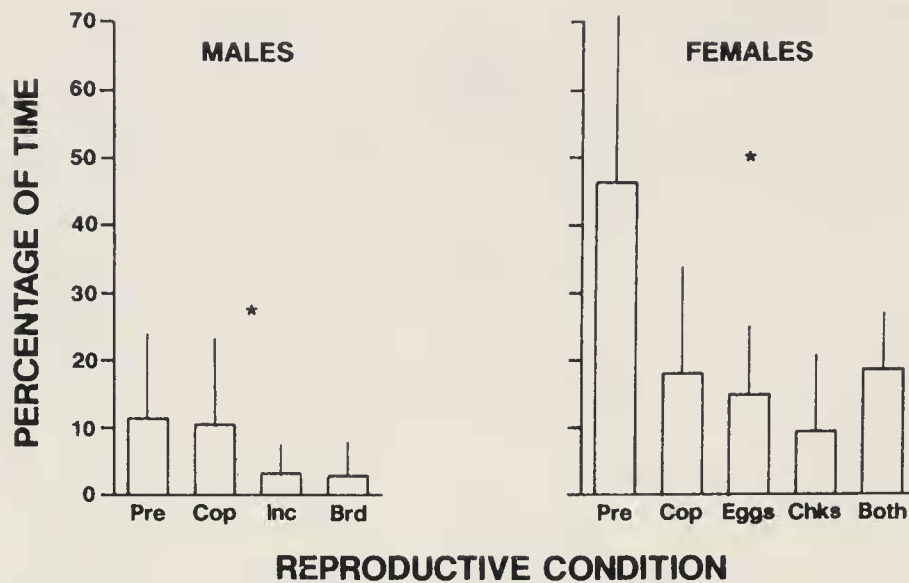
FIG. 4.   Percentage of total time spent off the pond by males and females as a function of reproductive condition. Abbreviations and sample sizes as in Fig. 1. Statistical significance: * = $P \leq 0.05$ that there was no difference between reproductive conditions in the percentage of time spent off the pond.

Location differences. — Jacanas spent part of their time on nearby lawns or pastures (this study) or on meadows or grasslands (western Costa Rica, pers. obs.). Males spent much less time off the Turrialba pond once they had eggs or chicks (Fig. 4). Females spent nearly half their time off-the-pond during the precopulation period but significantly less time off-the-pond after that (Fig. 4).

Grouped behaviors were used to compare off-the-pond and on-the-pond time budgets. The percentage of time males and females spent foraging was significantly greater when off-the-pond than when on-the-pond during all reproductive conditions (Fig. 5). The inverse was always true for the other somatic behaviors (Fig. 5). The percentage of time the two sexes spent in intraspecific and interspecific aggression either did not differ significantly between off-the-pond and on-the-pond or else was significantly greater when on-the-pond (Fig. 5). No other mating or parental behaviors occurred off-the-pond during our observations.

The effect of location on the time budgets of females was much more complex than for the males. When females had males with eggs and/or chicks, the females distributed their time differently depending on which male's territory they were in (Fig. 6). Although females in all three reproductive conditions tended to feed a greater percentage of time when in territories of males without offspring than when in territories containing eggs or chicks, these differences were not significant (Fig. 6). The fact that females did not consistently reduce their foraging in territories with eggs or chicks also can be seen by examining the females' foraging patterns before and after laying the five clutches that eventually produced chicks
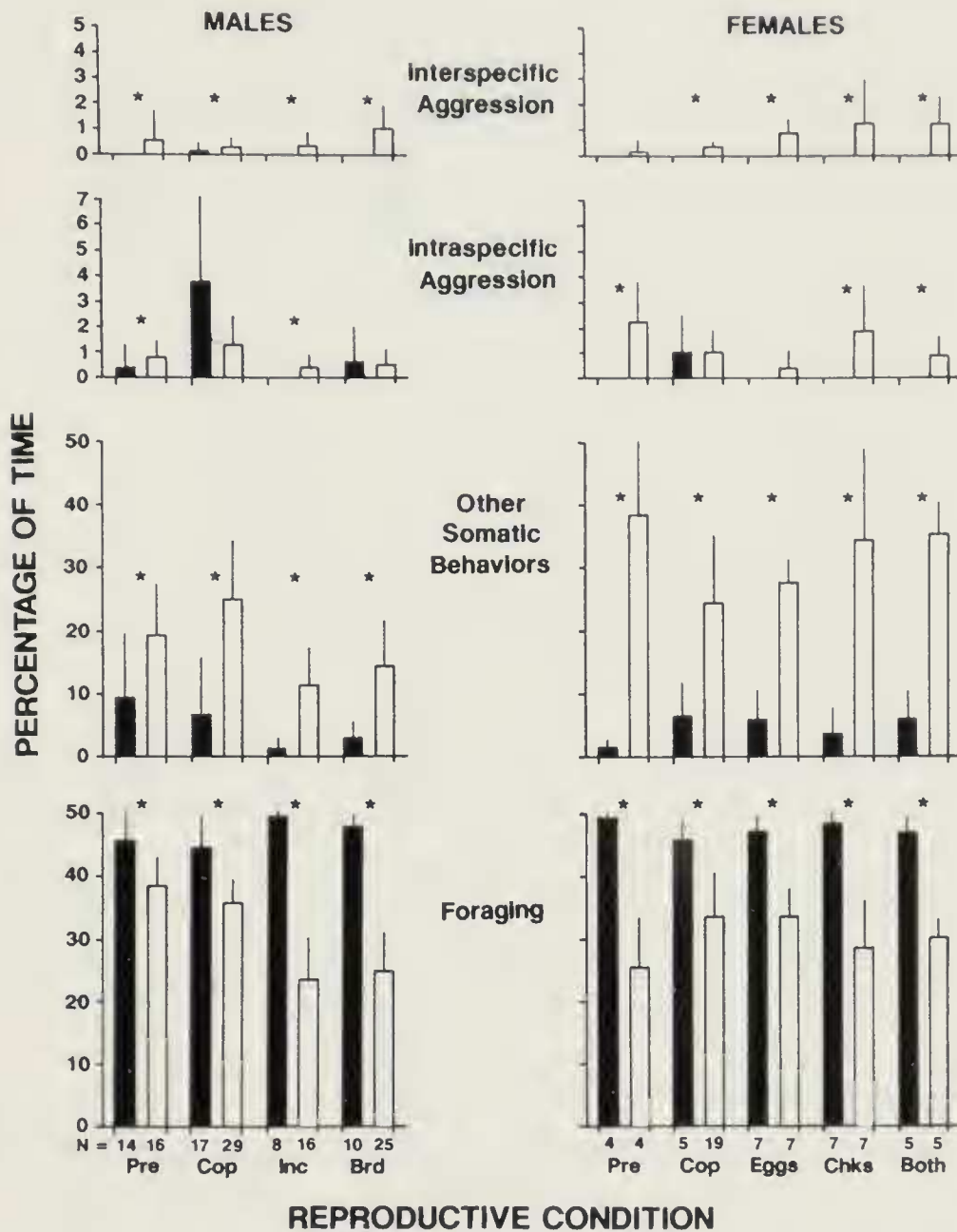
FIG. 5. Comparison of time budgets when males and females were in their territories (open bars) and when they were off the pond (solid bars). Abbreviations as in Fig. 1. Statistical significance: * = $P \leq 0.05$ that there was no difference between the percentage of time spent in a behavioral category when in their territories and the percentage of time spent in that category when off the pond.

(Table 2). The proportion of total female feeding time spent in the territory of the male who received the clutch did not change consistently from copulation throughout the nest cycle (Friedman two-way ANOVA; $\chi_r^2 = 1.2$, df = 2, $P = 0.691$).

Females in all three reproductive conditions spent significantly more time in other somatic behaviors when in territories containing eggs or chicks than when in territories with no offspring (Fig. 6). Preening and resting were the most frequent of these behaviors, and the tendency of females to perform them in territories containing eggs or chicks enabled the females to provide non-overt parental care in the form of predator
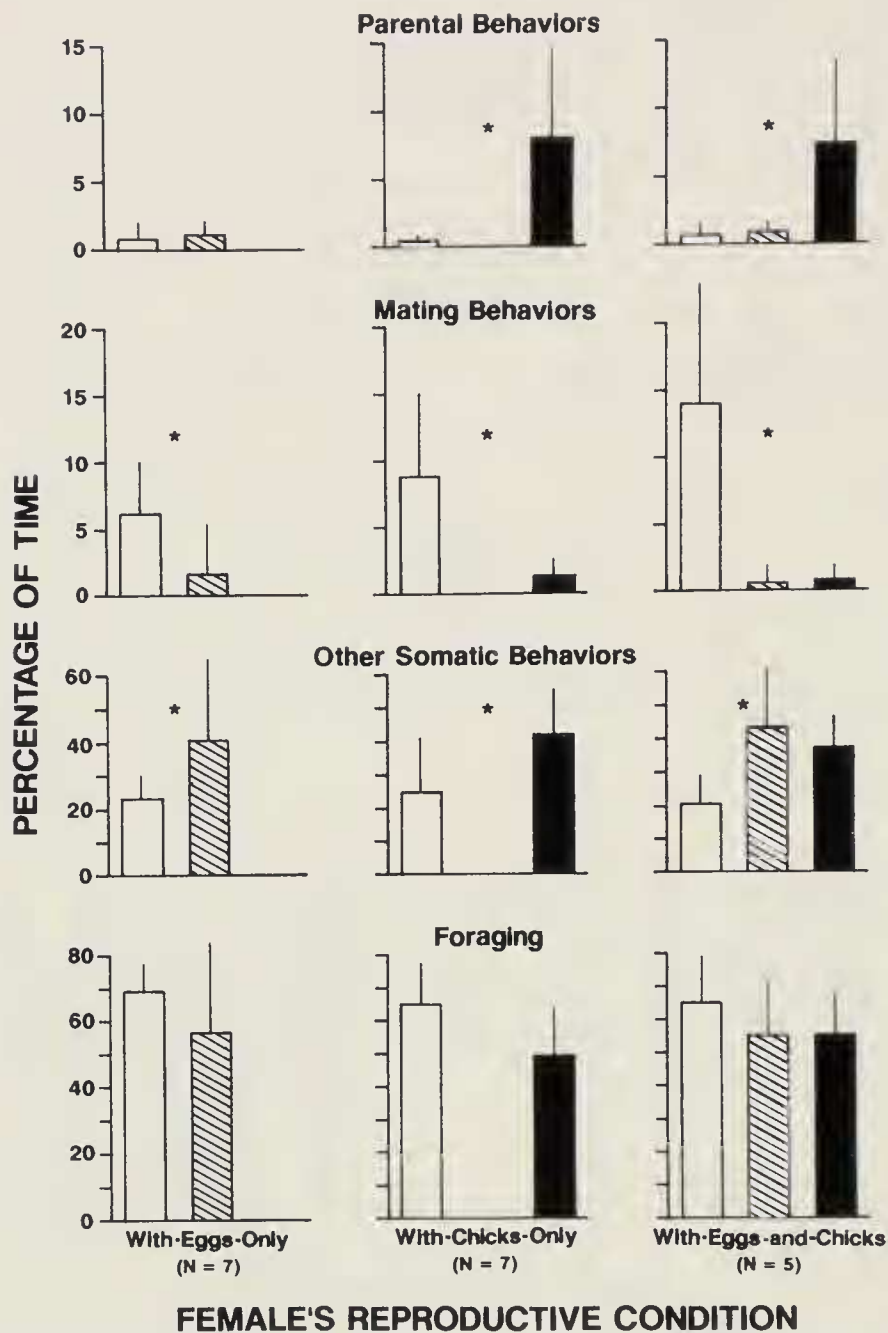
FIG. 6. Comparison of female time budgets during three reproductive conditions as a function of location. Open bars = in territory of male that had neither eggs nor chicks; hatched bars = in territory of male that had eggs; solid bars = in territory of male that had chicks. Statistical significance: * = $P \leq 0.05$ that there was no difference between the percentage of time females spent in a behavioral category when in territories of males in different reproductive conditions.

vigilance. As expected, mating behaviors were most frequent when females were in territories of males with no offspring, and parental behaviors were most frequent when females were in territories containing chicks.

Time of day differences.—Significant diurnal variation in time spent foraging occurred in all reproductive conditions for males (Fig. 7). During the precopulation and copulation periods, male foraging showed only slight mid-morning lulls. However, diurnal variation increased considerably in the incubation and brooding periods, with foraging peaking around midday (Fig. 7). Early morning and mid-to-late afternoon were

TABLE 2

PERCENTAGE OF TOTAL FEMALE FEEDING THAT WAS DONE IN TERRITORIES RECEIVING
CLUTCHES THAT EVENTUALLY PRODUCED CHICKS

Clutch number	Clutch status					
	Copulation		Eggs present		Chicks present	
	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD	N	$\bar{x} \pm$ SD
1	3	34.2 ± 14.5	3	41.0 ± 9.9	6	29.5 ± 16.4
2	6	33.6 ± 18.8	4	28.9 ± 9.8	1	58.8 ± 0.0
3	2	12.3 ± 2.6	2	42.2 ± 19.0	3	16.9 ± 3.2
4	5	5.7 ± 2.9	2	4.8 ± 3.7	4	9.0 ± 3.5
5	7	14.0 ± 10.7	1	27.5 ± 0.0	3	19.4 ± 11.0
Mean		20.0 ± 13.1		29.5 ± 15.7		26.6 ± 19.5

the coolest and rainiest parts of the daylight hours, respectively, and the times of greatest incubation and brooding (Fig. 7). The conclusion that parental demands, rather than changes in foraging efficiency, dictated the change in daily foraging pattern is supported by data for females, which were not observed to incubate, rarely brooded, and showed no significant diurnal variation in time spent foraging during any reproductive condition (Fig. 8).

In males, other somatic behaviors differed significantly with time of day during the incubation and brooding periods. Like foraging, these behaviors were less frequent early and late in the day as males devoted time to parental care (Fig. 7). Females exhibited no significant diurnal variation in time spent in other somatic behaviors during any reproductive condition (Fig. 8). Mating behaviors of both sexes showed significant diurnal variation during the copulation period, with the frequency of these behaviors generally being inversely related to the frequency of somatic behaviors (Figs. 7 and 8).

DISCUSSION

The mating system of the Northern Jacana is an example of resource defense polyandry (Emlen and Oring 1977) in which females gain access to several males by excluding other females from the males' territories. Pair formation in this species is much less a product of intersexual courtship than it is a product of intrasexual competition for territories. Males compete among themselves for breeding territories and females compete among themselves for control over the males and their territories. A male accepts as his mate the female who excludes other females from his territory, and females pair with males that hold territories within her ter-
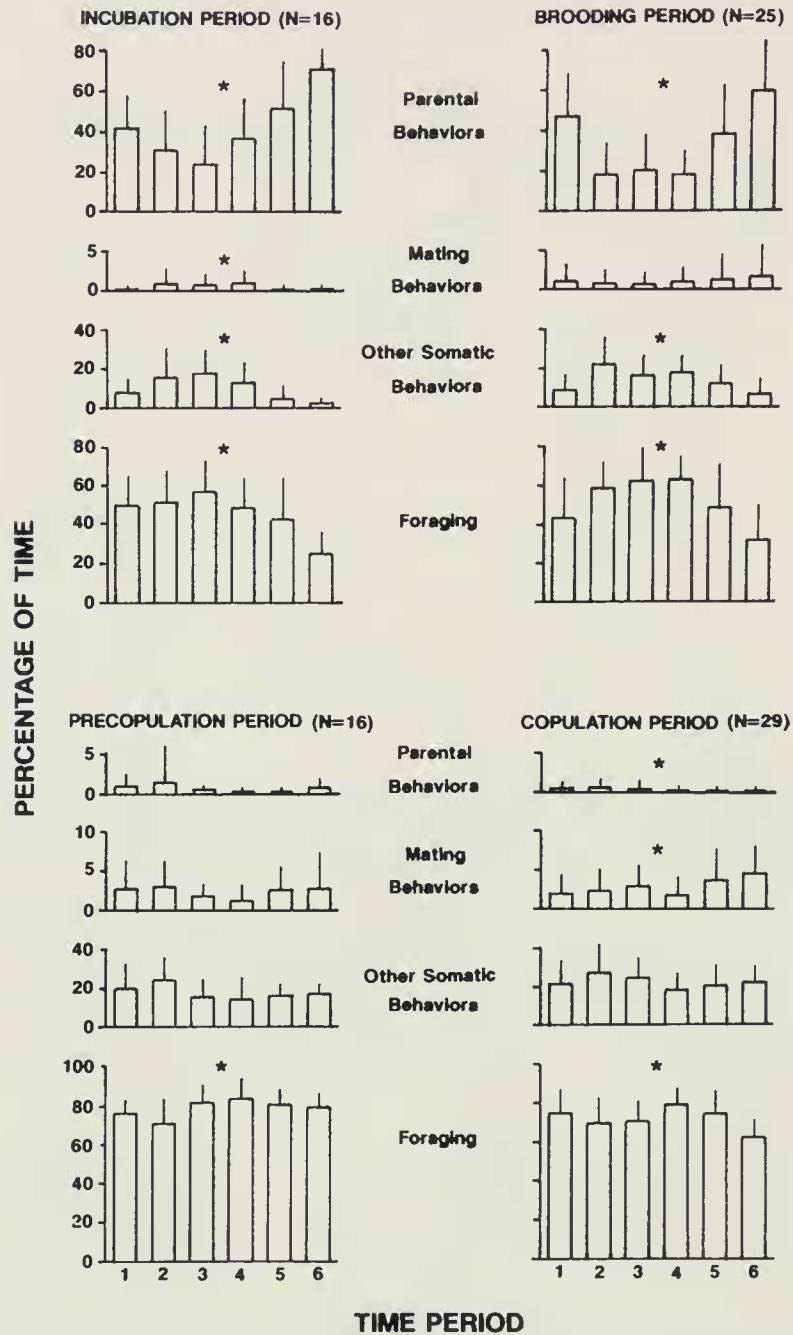
FIG. 7. Male time budgets during four reproductive conditions as a function of time. Time periods: 1 = dawn–08:00, 2 = 08:00–10:00, 3 = 10:00–12:00, 4 = 12:00–14:00, 5 = 14:00–16:00, 6 = 16:00–dusk, CST. Statistical significance: * = $P \leq 0.05$ that there was no difference between time periods in the percentage of time spent in a behavioral category.

ritory. At Turrialba, Northern Jacanas held territories throughout the year and their ownership changed infrequently. Except during these infrequent ownership changes, such a system ought to require little time expenditure devoted to mating behaviors, an hypothesis that is confirmed by our data. Neither males nor females spent more than 2% of their time in intraspecific aggressive encounters (Fig. 2). For both sexes, the majority of these encounters occurred in territories of males with neither eggs nor chicks, probably as a consequence of males wandering more widely when they were not incubating or brooding. Presenting-mounting and copulating consumed less than 1% of male time budgets and 4% or less of female
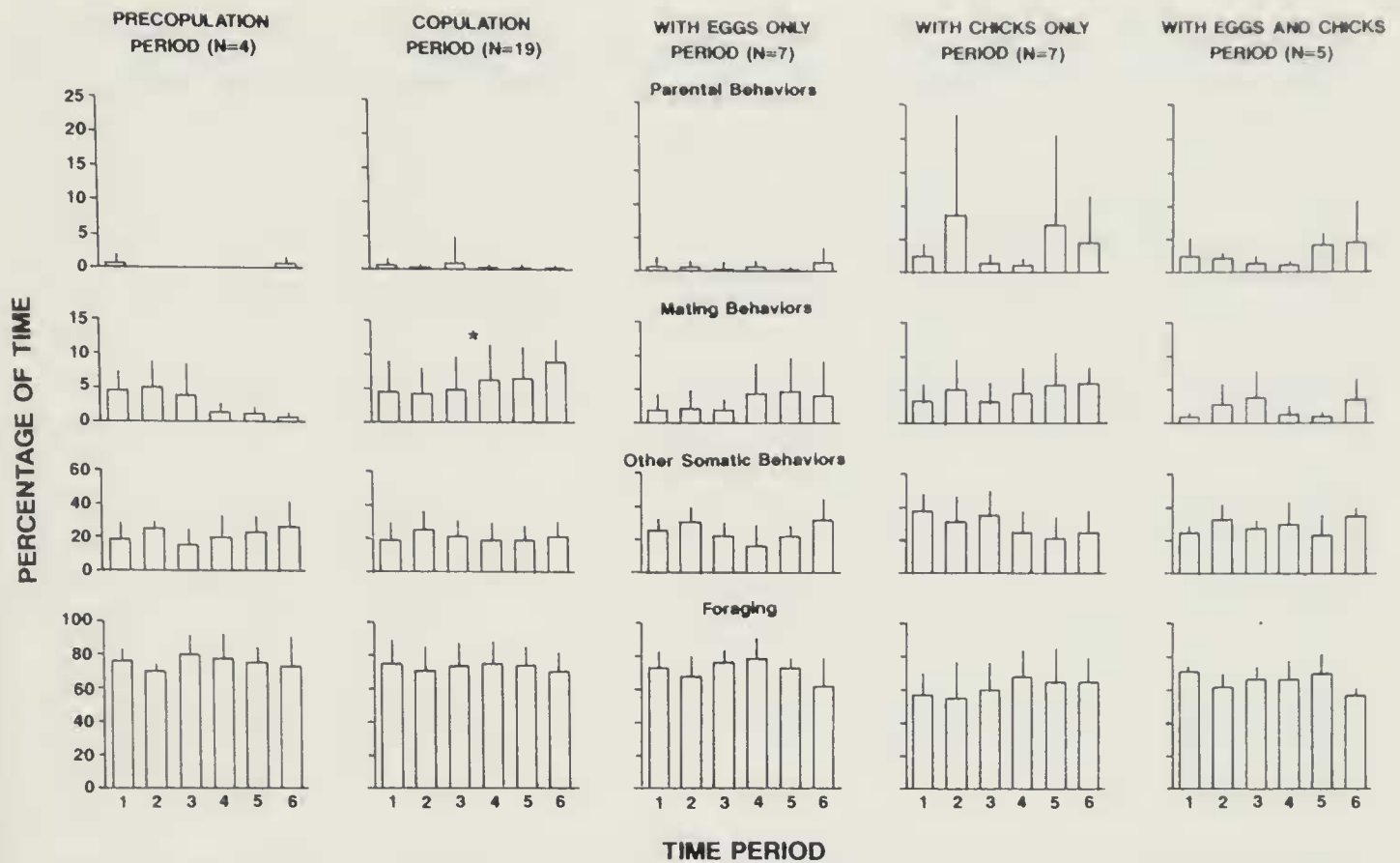
FIG. 8. Female time budgets during five reproductive conditions as a function of time. Time periods and statistical significance as in Fig. 7.

time budgets, with the peaks occurring as expected during the precopulation and copulation periods (Fig. 2).

The evolution of sexual differences in parental investment is prerequisite to the evolution of polygamy (Trivers 1972, Maynard Smith 1977). Polyandry should evolve when males can increase their fitness by assuming the bulk of parental duties while the female is free to regain the nutrient and/or energetic ability to produce replacement clutches (Emlen and Oring 1977). Thus, male and female jacanas should have different reproductive strategies that ought to be reflected as major differences in their time budgets, particularly in the time devoted to energy acquisition and parental duties.

Male foraging was high throughout the day during the precopulation and copulation periods, but once eggs or chicks were present the demands of incubating, brooding, and attending chicks resulted in greatly reduced foraging, particularly early and late in the day (Figs. 1 and 7). This reduction was associated with a decrease in time spent off-the-pond, most of which had been devoted to foraging (Figs. 4 and 5).

This decrease in male foraging probably had little effect on male fitness during the peak of breeding. Even with reduced time spent foraging during parts of the day, males seemed able to satisfy their energy needs during

the four weeks of incubation and 10 weeks of brooding. However, the presence of eggs or young chicks at times of the year with extensive rainy periods and cooler temperatures may require so much time incubating and brooding that the male has insufficient time to forage. It was during such weather conditions that females "reluctantly" brooded (the chicks usually had to force their way under the female's wings) and one male lost a set of chicks less than one week old because of his inattentiveness (Jenni and Betts 1978). These chicks hatched during an extensive rainy period; two disappeared after five days for unknown reasons, and the other two were preyed upon by a Purple Gallinule (*Porphyrula martinica*) while the parents were both away from the pond. The fact that several territorial birds seemed to be spending more time foraging off-the-pond than usual suggests that food abundance was relatively low on-the-pond, perhaps also because of the weather conditions. Low food availability on-the-pond may have produced a conflict in the male's time budget between his foraging needs and the parental care needed by his offspring, with the latter getting less than necessary. Certainly, it would be adaptive in such cases for the male to provide for his own survival needs in preference to those of his chicks, which could not have survived without him anyhow.

The foraging patterns of males and females differed in several ways. Female foraging remained high throughout the day regardless of reproductive condition and was highest during the precopulation, copulation, and with-eggs-only periods when the energetic demands of egg formation should be highest. Thus, while male foraging is reduced by parental duties, females can continue to acquire energy and nutrients for additional clutches. That this is potentially beneficial to the male is evidenced by the history of one male who received three clutches in 1974. Although he abandoned his first clutch when his mate was replaced, his new mate provided him a clutch two months later. This clutch was lost before hatching, and he received a replacement clutch within two weeks.

Another important aspect of female foraging is the amount of foraging done in territories containing chicks. A potential benefit of polygamy is reduced competition between adults and offspring for food if the polygamous parent abandons the territory (Pitelka et al. 1974). Female jacanas are significantly larger than males (Jenni and Collier 1972) and have greater metabolic maintenance demands, which may contribute to the greater foraging time observed in females of this species. When food abundance is low, which by circumstantial evidence seemed to occur at irregular intervals at Turrialba, it would seem appropriate for females to concentrate foraging elsewhere rather than in territories with chicks. Although females did forage a smaller proportion of the time they were in territories with chicks (Fig. 6), they also spent more total time in these

territories. Thus, there was no overall reduction of foraging, at least in the territories of the five broods produced during this study (Table 2). A reduction in foraging and hence in competition may occur when food abundance is low, but we have no data to test this possibility.

The male is responsible for the majority of parental care. Once he received a clutch, a male's daily time budget changed to include extensive periods of incubation, brooding, and walking with the chicks (Fig. 3), especially during the cool early mornings and often rainy late afternoons (Fig. 7). There was generally a corresponding decrease in the frequency of male foraging, other somatic behaviors, and time spent off-the-pond (Figs. 4 and 7). By spending more time on-the-pond, the male probably provided the eggs and chicks better protection from potential predators.

The females' reproductive strategy is one of providing eggs and predator protection. High levels of foraging allowed for the former and spatial variation in the performance of a variety of behaviors allowed for the latter. Females concentrated preening, resting, and walking in territories with offspring (Fig. 6). In choosing these territories for these maintenance behaviors, the females provide the potential for predator protection, and this may have been largely responsible for the involvement of females in so many interspecific aggressive encounters in territories containing chicks (Fig. 6).

Of the various hypotheses for the adaptiveness of classical polyandry, our data best support the replacement clutch hypothesis for polyandry in the Northern Jacana, although they are insufficient by themselves to eliminate other hypotheses completely. Clutch loss in the Turrialba population was high, as predicted by this hypothesis. Based on 1–2 month observations of this population between 1963 and 1973, Jenni (1974) estimated nesting success at 50% or less. Four of eight clutches laid in 1974 were lost before or soon after hatching, and only one chick from each of the other clutches remained by the end of the study. Osbourne (1982) reported total clutch loss in 84.6% of 52 Wattled Jacana nests. Although temperate zone, polyandrous Spotted Sandpipers had a hatching success of only 39% over nine years (Oring et al. 1983), tropical shorebirds, in general, experience lower nesting success and greater replacement opportunity than more northern species (Erckmann 1983).

Inherent in the replacement clutch hypothesis is the assumption that polyandrous females, freed from most parental duties, can rapidly replace lost energy stores and lay additional clutches. However, this assumption cannot be tested simply by comparing clutch replacement rates between polyandrous and monogamous, biparental species. Although a female may be physiologically capable of producing another clutch, doing so may be delayed by such factors as a change of mates, territorial challenges from

other females, and weather variations. In Spotted Sandpipers the laying rate of additional clutches was affected by the rate of nest predation and the availability of males but not by food abundance, and females were able to begin replacing clutches as soon as the day after a clutch was lost (Lank et al. 1985).

Comparison of clutch replacement rates between polyandrous and monogamous, biparental shorebirds is further clouded by the possibility that rapid replacement also may be important to monogamous species. Killdeers suffer clutch losses as high as 64% (Mace 1971), and females spend significantly less time in parental duties and more time foraging than males (Brunton 1988). This may enhance production of additional clutches; Killdeers renest up to three times in a season (Mundahl 1982, Brunton 1988). Males of other monogamous shorebirds also contribute significantly more time to parental duties than females even though biparental care is necessary (Hussell and Page 1976, Miller 1985), but whether this is related to the rate of clutch replacement is not known.

In this study, we have clutch replacement data for only one renesting; the new clutch was started 19 days after the female started the first clutch and 15 days after its loss. One female Wattled Jacana laid four clutches for the same male over a 45-day period (Osbourne and Bourne 1977), and another laid six clutches for two males over a 60-day period (Osbourne 1982). The shortest replacement time was 10 days after starting the first clutch and only two days after the first clutch disappeared. Thus, replacement time varies considerably within the tropical jacanas, and we do not believe knowledge of the factors producing this variation is sufficient at this time to rule out the replacement clutch hypothesis on the basis of a comparison of replacement times of polyandrous and monogamous females.

Conversely, the replacement clutch hypothesis is supported by our female foraging time data. This hypothesis predicts that time spent foraging by females should be higher than for males and should be higher than in species which usually lay only one clutch per season. The first prediction is met by our data. Although initially similar, time spent foraging by males and females became significantly different after laying as male foraging time decreased by one-third (Fig. 1). Comparison with other species is not possible because we have no data on food abundance which can affect time spent foraging (Maxson and Oring 1980).

The female energetic stress hypotheses for the adaptiveness of polyandry suggest that severe energy stress of the female makes her more likely to desert the male than help with parental care (Lenington 1984). But Erckmann (1983) and Maxson and Oring (1980) argue that food scarcity should select for biparental incubation rather than desertion by either parent,

and female Spotted Sandpipers did not incubate less when food was scarce (Maxson and Oring 1980, Lank et al. 1985, Oring and Lank 1986). Our data do not support these hypotheses for the Northern Jacana. First, the rare occurrences of female brooding occurred just when food was least abundant. Second, female foraging time decreased after laying (Fig. 1), rather than increasing as predicted by this hypothesis (Lenington 1984). Third, our females increased resting time after laying (Fig. 1).

The uniparental care hypotheses also are not supported by our data for the Northern Jacana. Females did not reduce the absolute amount of time they fed in a territory once eggs or chicks were there (Table 2). However, this observation is based on the history of only five clutches, and we do not have corresponding quantitative data on food supply.

The limited amount and incompleteness of published data make rigorous testing of these hypotheses difficult at best. Furthermore, there are not yet sufficient data available to conclude that the various mating systems identified as polyandrous are in fact identical (Oring 1986). Attempting a single explanation for the adaptiveness of classical polyandry is premature before we know we are dealing with a single type of mating system. Clearly we need more descriptive data on the understudied, presumptively polyandrous species.

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